Title: Colonies of *Acropora formosa* with greater survival show conserved calcification rates

Authors: Vanessa Clark, Sophie Dove

Affiliations:

School of Biological Sciences, The University of Queensland, St. Lucia, Queensland 4072, Australia

ARC Centre of Excellence for Coral Reef Studies, The University of Queensland, St. Lucia, Queensland 4072, Australia

Email of communicating author: vanessa.clark@uq.net.au

Keywords: *Acropora formosa*, calcification, tissue biomass, epigenetics, reciprocal transplantation

Abstract

Coral reefs are facing increasingly devasting impacts from ocean warming and acidification due to anthropogenic climate change. In addition to reducing greenhouse gas emissions, potential solutions have focused either on reducing light stress during heating, or the potential for identifying "super corals" that survive and reproduce under heat stress. These studies, however, have tended to focus on the bleaching response of corals, despite recent evidence that bleaching sensitivity is not necessarily linked to coral mortality. Here, we explore how survival, potential bleaching and coral skeletal growth (as branch extension and densification) varies for conspecifics collected from distinctive reef zones at Heron Island on the Southern Great Barrier Reef. A series of reciprocal transplantation experiments were undertaken using the dominant reef building coral (*Acropora formosa)* between the highly variable 'reef flat' and the less variable 'reef slope' environments. Coral colonies originating from the reef flat had higher rates of survival and thicker tissues but reduced rates of calcification than conspecifics originating from the reef slope. The energetics of both benefited from greater light intensity offered in the shallows. Reef flat origin corals moved to the lower light intensity of reef slope reduced protein density and calcification rates. For *A. formosa*, genetic difference, or long-term entrainment to a highly variable environment, promoted survival of reef flat conspecifics at the expense of calcification. Such a response divorces coral resilience from carbonate reef resilience, and would be exacerbated by any reduction in irradiance. As we begin to discuss interventions necessitated by the CO_2 that has already been released to the atmosphere, we need to prioritise our focus on the properties that maintain valuable carbonate ecosystems. Rapid and dense calcification by corals such as branching *Acropora* is essential to the ability of carbonate coral reefs to rebound following disturbances events.

Introduction

Primary (skeletal expansion) and secondary (skeletal densification) calcification by reef-building corals is critical to reef construction and other services provided by coral reef ecosystems (Spurgeon 1992). Environmental impacts on rates of net coral calcification often differentiate ecosystems that are labelled carbonate coral reef ecosystems and those that are labelled coral reef communities (Kleypas et al. 1999a). The ephemeral nature of reef-building by Scleractinian corals has, however, enabled corals to survive mass extinction events (Stanley 2006). Calcification is energy expensive (Cohen and Holcomb 2009), and in some environments, it may be necessary to redirect energy investment away from calcification in order to facilitate coral survival (Leuzinger et al. 2012). Here, we evaluate drivers such as putative epigenetic responses and exposure to reduced light levels over summer and their influence on primary and secondary calcification for the branching coral, *Acropora formosa* (Dana, 1846). *A. formosa* is present in diverse zones of a coral reef where it contributes to the 3-dimensional structure and carbonate accumulation within coral reef ecosystems (Veron 1993).

Underwater marine heat waves are increasing globally and are impacting multiple ecosystems including the Great Barrier Reef (Hoegh-Guldberg 1999; Hughes et al. 2018a; Smale et al. 2019). Initially, coral bleaching observed over a large area drew our attention to the fact that ocean warming was negatively affecting coral hosts and their endosymbiotic dinoflagellates (Hoegh Guldberg and Salvat 1995). More frequent and intense thermal heatwaves are now associated with mass coral mortality, where corals die irrespective of their apparent bleaching susceptibilities (Hughes et al. 2018b). Past emission of CO_2 from fossil fuel burning, and the lag between emission and ocean impacts, mean that future reefs will almost certainly be exposed to thermal events that will occur with greater frequency and greater intensity than those we have witness to date (Hoegh-Guldberg et al. 2019). The adoption of CO_2 mitigation pathways such as that agreed in Paris at the United Nations Climate Change Conference in 2015 will significantly reduce ocean acidification and hence impacts on coral reef ecosystems (Magnan et al. 2016). Eventuating conditions are nonetheless likely to have impacts on coral communities (Albright et al. 2016). Impacts that may affect the rate of net calcification and frame work-building on a coral reef, thereby threatening key services provided by these ecosystems (Hoegh-Guldberg et al. 2007).

The degree to which these ecosystems are threatened under reduced CO_2 emission scenarios such as RCP2.6 (IPCC 2014) is nonetheless debated with some arguing that epigenetics can accelerate coral adaptation either naturally (Palumbi et al. 2014) or via assisted evolution (Van Oppen et al. 2015; Putnam et al. 2016). In such studies, bleaching susceptibility is often viewed as interchangeable with mortality susceptibility (van Oppen et al. 2011; Puill-Stephan et al. 2012; Levin et al. 2017; Cleves et al. 2018), and the costs (in terms of skeletogenesis) associated with "adaptation" are rarely considered (Hoegh-Guldberg et al. 2011; Pandolfi et al. 2011). Other research efforts have focused on potential solutions associated with reducing light stress to inhibit thermal bleaching (Jones et al. 2016). Such potential solutions assume corals and their endosymbionts do not acclimate sufficiently rapidly to reductions in light to obviate the benefits of reducing light on symbiont excitation pressure at PSII reaction centres (Iglesias-Prieto and Trench 1997), with excessive excitation driving the formation of reactive oxygen species that can trigger a bleaching response in corals (Smith et al. 2005; Dove et al. 2006). At the same time, they assume that the reduction in light and hence reduced photosynthesis from periods of shading is not important to coral host coral energetics (Fisher et al. 2019). In the present study, we examined the potential for either of these solutions to translate into increased survival potential and optimal framework building in response to summer conditions 2017-2018. We also argue that, if they are not beneficial under current conditions, then they are unlikely to be beneficial under future climate conditions.

The study was done at two different reef locations, (a) the shallow reef flat (1-3 m) and (b) the deeper reef slope (7-8 m) of Heron Island, on the Great Barrier Reef. Colonies from the reef flat sites experienced a large diel range and variability in sea water chemistry (e.g. pCO_2), temperature and light intensity, which is associated with the large tidal range (3m) and the ponding of reefs at low tide (McGowan et al. 2010; Santos et al. 2011, and Kline et al. 2012, 2015). Periods of excessively high (in summer) or low (in winter) temperatures associated with ponding can inhibit the efficiency of photosynthesis (Coles and Jokiel 1977) given Heron Island's high latitude location. Over such periods, corals growing at Heron Island potentially limited in their heterotrophic uptake capacity may be forced to consume previously deposited biomass to facilitate genet survival (Anthony et al. 2009; Grottoli and Rodrigues 2011). Survival in such environments may therefore favour organisms with larger biomass per unit surface area (Szmant and Gassman 1990; Grottoli et al. 2006), a

property that in turn may be facilitated by reductions in coral expansion and/or in rates of secondary calcification (Anthony et al. 2002; Tanaka et al. 2007).

By contrast, on the reef slope , temperature and pCO_2 conditions are relatively stable due its proximity and exchange with external ocean waters (Albright et al. 2015). Light, however, attenuates significantly with depth and can constrain phototrophy. On the other hand, the increased exposure to high energy of waves tends to limit the potential for net colony expansion, especially for corals that deposit less dense skeletons over the long term (Allemand et al. 2011). The combination of fragmentation, driven by high wave energy and rapid rates of skeletogenesis can spread the risk of genotype mortality across a larger area (Highsmith 1982). Therefore, it may be hypothesized that, in general, fast growing morphotypes are more frequently associated with high energy locations; whilst fleshier morphotypes, that tend to invest more in tissue than skeletal expansion, are associated with more marginal, low energy habitats (Hoogenboom et al. 2008).

Epigenetic memory potentially offers corals and other organisms a mechanism for responding to climate change at rates that are greater than one might expect based on their average generation times (Van Oppen et al. 2015; Putnam et al. 2016 vs Hoegh-Guldberg et al. 2002). Epigenetic memory is a mechanism through which the transcriptional responses of parent cells to environmental stimuli are maintained as the favoured set of transcriptional responses in descendant cells irrespective of environmental stimuli (Klosin et al. 2017). In this sense, epigenetic exposure to highly variable light and/or temperature environments, can lead to transcriptional behaviours in parent cells that are retained in descendant cells. Descendant cells are therefore less likely to be responsive to their immediate environment, but rather retain the properties and behaviours that enabled parent cells to survive and divide in their relatively hostile historic environment. The long-term prior experience of a coral genet that settled and grew to adulthood in a highly variable environment, does, in at least some cases, appear to provide an epigenetic entrainment that increases the survival potential of corals experimentally exposed to regionally anomalous increases in temperature (Oliver and Palumbi 2011; Grottoli et al. 2017; Thomas et al. 2018). Some such corals have been referred to as “super corals” (Grottoli et al. 2017; Darling and Côté 2018). This term has been used in reference to naturally occurring robust species of corals, conspecifics that have settled and developed into adult colonies in highly variable environment (Oliver and Palumbi 2011; Grottoli et al. 2014, 2017), but also to describe the artificial manipulation of corals through

the formation of chimeras (van Oppen et al. 2011; Puill-Stephan et al. 2012), editing of larval genes (Cleves et al. 2018), or the insertion of artificially developed symbionts (Levin et al. 2017). “super corals” are first and foremost described as having a higher thermal tolerance in the face of bleaching, requiring a more extreme temperature to induce the loss of symbionts (Hoogenboom et al. 2008; Grottoli et al. 2017). The cost of this bleaching resilience, however, in terms of both aspects of skeletogenesis has not been explored, despite the fact that the link between bleaching sensitivity and greater host survival is often assumed, along with the assumption that corals conspecifics that do not bleach are healthier than those that do bleach (Berkelmans and Van Oppen 2006; Howells et al. 2013; Lirman et al. 2014).

Implicit to coral health is the assumption that their endosymbiotic dinoflagellates are strict photo-autotrophic obligate mutualists, which are incapable of translocating organic carbon from host to symbiont (Rowan and Knowlton 1995; Rowan et al. 1997; Mieog et al. 2009) . Relatively recent advances in the literature, however, indicate that this is incorrect as all chloroplast-containing dinoflagellates, inclusive of Symbiodiniaceae, are facultative heterotrophs (Steen 1987; Mulholland et al. 2018). At least some are capable of phagotrophy, but all are capable of osmotrophy (Flynn et al. 2013). And hence, all, under the appropriate changes to the environment, can become parasitic on their coral hosts. Several studies clearly demonstrate that non-bleached corals can be even less healthy than their unhealthy bleached counterparts. Non-bleached conspecifics can show higher susceptibility to polyp mortality when phototrophic capacity is eliminated (Steen 1986, 1987). Similarly, bleached hosts that house thermally tolerant symbionts can show reduced extension rates, lower lipid densities, and decreased reproductive output both during and after the advent of a thermal event (Jones and Berkelmans 2010, 2011). The visual nature of mass coral bleaching has led us to overly focus on the symbiont response, as opposed to realising that the host appears to be energetically deprived when exposed to thermal stress often irrespective of whether symbiont population densities are maintained. Recent observations of prolonged thermal events that lead to mass coral mortality irrespective of the documented bleaching susceptibility of the taxa involved (Hughes et al. 2018b) would also seem to argue for a new functional definition for a “super coral”. One that focusses directly on survival and growth of corals as opposed to their brown colour and bleaching sensitivity.

We ran reciprocal field experiments on *Acropora formosa* growing in two distinct environments; on the highly variable shallow reef flat and in a less variable, but slightly

deeper outer reef slope of Heron Island, on the southern Great Barrier Reef, Australia. We aimed to test an alternative hypothesis that corals survive highly variable environments because they engage in conservative extension rates that enable them to invest their energy into tissue maintenance and production. We further aimed to explore whether there was any influence of prior environmental history (i.e. potentially epigenetic memory) that might constrain the responses of colonies of *A. formosa*. Specifically, we sought to: (i) determine whether higher exposure to variability in prior life history increases coral survival irrespective of the characteristic of the new environment; (ii) Whether properties that potentially increase survival are traded for reduced rates of calcification; (iii) whether light reductions associated with alteration in depth and reef location, led to a rapid acclimation response or not and whether a potential decrease in energy acquisition occurs as corals face changed environmental conditions.

Materials and Methods

Study Site

Heron Island (23°27'S, 151°55'E) is a lagoonal platform reef which is part of the Capricorn Bunker group located on the southern end of the Great Barrier Reef, Australia. Past sea surface temperatures (SST) for the sea surrounding Heron Island had a maximum monthly mean (MMM) of 27.3°C (between 1985 and 2001; Weeks et al. 2008). This is also the MMM used to determine hotspots and degree heating weeks (DHW), and thereby exposure to thermal stress (Liu et al. 2014). Heron Island has a semi-diurnal tide cycle, which drives a large scale variation in temperature, oxygen, and carbon dioxide (Kline et al. 2012). For this study, sites were either located in reef flat or outer reef slope on the southern side of Heron Island tides. Conditions on the reef flat (1-3m, Gourlay and Jell 1992) are highly variable with regular periods of ponding with minimal or no inward or outward exchange of water (Kinsey 1967; Jell and Flood 1978; Potts and Swart 1984; Jell and Webb 2012; Georgiou et al. 2015). The reef slope sites (depth 7-8m at mid-tide, Harry's Bommie) were on the outer margin of the reef nearby Wistari channel and hence exposed to well mixed ocean waters along with significant wind and wave activity (Bradbury 1981; Connell et al. 1997). Brown et al. (2018) conducted studies at similar sites on Heron Island finding that mean photosynthetically active radiation (PAR) was two to three times higher on the reef flat than the reef slope throughout the year, while mean temperature remained relatively similar between sites seasonally. Heron Island is dominated by *Acropora spp.* (Santos et al. 2011; Brown et al. 2018) which are typically fast growing under normal conditions, and as a result can rapidly recolonise after events that have led to reef degradation (Highsmith 1982), especially via fragmentation. Making them fundamental in maintaining positive carbonate balances within coral reef communities.

Reciprocal Transplantation

Fragments (7-10cm) of *A. formosa* were collected from different colonies at each location ('Flat' n=125; 'Slope' n=125) in late September 2017. Fragments were randomly collected from the growing tips of colonies, fragments with axial branches or damaged apical corallites were excluded. While these were selected from different colonies to avoid pseudo-replication it was not tracked. Corals were kept in flow through aquaria under a shade cloth during initial measurements and preparation for the different experimental treatments. All fragments were trimmed to 7cm using bone cutter scissors. A total of 25 fragments from each location (Flat, Slope) were selected to represent initial measurements, theses were stored at -

20°C until being analysed either at Heron Island Research Station and/or the University of Queensland. The remaining fragments had a hole drilled ~1cm from the base of the nubbin for ease of attachment to live rock. Ties through the hole were used to stabilise coral nubbins and reduce algal growth. Nubbins were randomly assigned to treatments in a fully crossed design, corals originating from the reef flat were either returned to the reef flat ("Origin[Flat]/ Transplant[Flat]", n=50), or transplanted to the reef slope ("Origin[Flat/ Transplant[Slope]", n=50), and corals originating from the reef slope were either returned to the reef slope ("Origin[Slope]/ Transplant[Slope]", n=50), or transplanted to the reef flat ("Origin[Slope]/ Transplant[Flat]", n=50). Once attached to live rock corals were deployed on metal frames at each location in late September 2017. The live rocks with nubbins attached were collected in late November 2017 for observation, all dead corals were removed (n=24) prior to redeployment. Final collection of the fragments was conducted in mid-February 2018, each nubbin had final buoyant weight measurements taken before being stored at -20°C until further analysis could be undertaken. Specific methodologies for individual measurements are described below. All physiological measurements, apart from buoyant weight, were reported as total change over the experimental period based on the average value calculated from the 25 fragments collected and processed at the beginning of the experiment.

Physiological analyses

Calcification rates were calculated from initial and final buoyant weight measurements of each individual fragment. Buoyant weight was measured using methods described by Spencer Davies (1989) and Jokiel et al. (2008), and reported as measured weight, not converted assuming a density for the skeleton. Coral tissue was removed from the skeleton by airbrush using 0.06 M phosphate buffer solution (PBS). Skeletons were then cleaned using a 10% bleach solution to remove any residual tissue. If corals had any tissue die-back this was marked on skeletons in preparation for living surface area analysis. Fragments were rinsed and dried at 70°C for two hours. Methods described in Bucher et al. (1998) were used for determining bulk volume.

The modified double wax dipping method described by Holmes (2008) was used to measure the surface area of living tissue. Paraffin wax was heated to 65°C, and coral fragments were maintained at room temperature throughout. This method has been shown to give the most accurate surface area estimation compared to X-ray CT scanners for Acroporid corals (Naumann et al. 2009; Veal et al. 2010).

The coral tissue in PBS was centrifuged at 4500rpm for 5 minutes (3K15 Sigma laborzentrifugen GmbH, Osterode, Germany), to separate the symbiont pellet. The resulting supernatant was stored in two parts to allow for protein and lipid analyses. For protein analyses the supernatant was analysed with a spectrophotometer (Spectramax M2 Molecular Devices, California, USA), using absorbance values at 235nm and 280nm. Protein concentrations were then calculated using equations in Whitaker and Granum (1980). For lipid analyses the supernatant was stored at -80°C overnight. Frozen samples were placed in a freeze dryer (Coolsafe 9l Freeze Dryer Labogene, Allerød, Denmark) at -110°C for 24 to 48 hours until all moisture was removed. Total lipid extraction from each sample was conducted using methods described in Dunn et al. (2012).

Mortality

Fragments in the reciprocal transplant could only be identified as dead during collection periods, at which point they were removed from the live rock. At the midway point of the study, 24 corals were classified as dead and removed, with one additional coral was removed due to mortality at the end point of the study. A coral fragment was classified as dead if it lacked coral tissue and had been colonised by algae. Dead fragments were excluded from physiological analyses.

Tissue dieback on all live fragments was also assessed at the end of the experiment. Approximately 80% of reef flat transplants, and 77% of reef slope transplant experienced a small amount of dieback near the point of attachment of their bases to the live rock. Algal growth was also apparent in some cases (fig 1a), and the absence of coralites and tissue in others (fig 1b). This was marked and accounted for when conducting live surface area measurements. Additionally, 5% of reef slope transplants exhibited tissue dieback beyond the attachment region but not total mortality, these were also excluded from further analyses.

Fig1 *Acropora formosa* nubbins from the reef slope transplant (a), and reef flat transplant (b) locations. Zip-ties represent origin locations (slope = blue, flat = red). Tissue dieback can be observed at base of nubbins where zip-ties have been attached, differential levels of dieback are due to a lack of uniformity in the live rock corals were attached to. The red circle in (a) highlights dieback with algal growth, and in (b) highlights dieback with the absence of coralites and tissue.

Environmental Variables

Field environmental variables were measured using temperature (Hobo pendent logger Onset, MA, USA), and photosynthetically active radiation (PAR; Odyssey logger Dataflow systems LTD, Christchurch, NZ) loggers. Three PAR and three temperature loggers were placed at each location (reef slope, and reef flat) each within 10 metres of the metal frames on which the corals were attached. On the reef slope two of the three PAR loggers failed and as a result only one set of data was able to be used for analyses. Temperature loggers collected data as hourly means; PAR loggers collected data as integrated values every 2 hours. For analyses, 24h daily means, 25th percentile (Q1) and 75th percentile (Q3) were

determined for temperature, but 12h (6h – 18h) daytime mean, Q1 and Q3 were determined for PAR.

Statistical Analyses

All statistical analyses were conducted with R version 3.6.2 software (2018), figures were created using the ggplot2 package (Wickham 2016)and sjplot package (Lüdecke 2014). Data was assessed for normality and homogeneity of variance through visual inspection of Q-Q plots and residual vs fitted values prior to analysis. All physiological data (bulk volume (BV), living surface area (LSA), buoyant weight (BW), total protein, and total lipids) was initially calculated as total change over time, however after comparison of initial bulk volume between origin locations this was converted to percentage change. This meant that final reported values accounted for the basal variability in bulk volume between fragment dependent on their location of origin. Linear mixed effects (LME) models were then developed using a stepwise procedure, Akaike information criterion was applied in each case to select the model with the best fit. Models were built up in order of increasing complexity in order to explore trades by fixing variables (Table 1). The function Anova (John et al. 2020) was applied to models, with the type 2 or 3 selection of treatment of sum of squares based on whether optimal models suggested significant interactions amongst variables.

For physiological analysis, model response variables were; BV, LSA, BW , total protein, and total lipids all of which were continuous. Of the fixed predictors, origin and transplant were categorical, while the remaining (BV, LSA, and BW) were continuous. Due to collinearity as measured through variance inflation factor (VIF), covariates BV and LSA were identified as interchangeable in subsequent models, the model with the best fit was chosen as previously described. All physiological analysis and mortality models included live rock as a random effect, which refers to the live rock on which the coral was placed, this remained constant throughout the experimental period.

Mortality was analysed as a single data point; this was applied to a mixed effect logistic regression (GLMER) in order to take the random effect of live rock into consideration. Laplacian approximation was used to determine the best fit model. The full and best fit models are shown in Table 1.

A linear model was used to compare environmental variables (Temperature and PAR) between each site (Flat and Slope) over the four-month experimental period. The daily mean,

and interquartile range (IQR, between Q1 and Q3 as previously described), as an indication of variability, were both analysed for temperature and PAR, full and best fit models are shown in Table 1, with date and location as categorical predictors. Degree heating weeks (DHW) were calculated using Q3 to measure heat accumulation over the experimental period, calculations were based on theory from NOAA (Liu et al. 2014) where heating weeks accumulate when temperatures rises above MMM +1.

Table 1 Response and predictor variables for the initial and best fit models described in statistical analysis section, as well as the type of statistical analysis used. Underlined predictors of the best fit models indicate significant effects (P<0.05). The direction of these significant effects is indicated in brackets, for continuous predictors, a positive significant effect is shown (+), and for categorical predictors the comparison of group means is shown. Transplant, Sh = Shallows, D = Deep; Origin, F = Flat, and Sl = Slope. The direction of interaction effects are not described in this table. Variables are shortened in model outputs; bulk volume = BV, living surface area = LSA, buoyant weight = BW.

Response Variable	Predictors (Initial Model)	Predictors (Best Fit Model)	Statistical Analysis
Mortality	Transplant * Origin	Origin **(F<Sl)**	GLMER
Bulk Volume	Transplant * Origin	Transplant **(Sh>D)** + Origin **(F<Sl)**	LME
Living Surface Area	Transplant * Origin + BV	Transplant **(Sh>D)** + Origin **(F<Sl)** + BV **(+)**	LME
Buoyant Weight	Transplant * Origin + BV/LSA	Transplant * Origin + LSA **(+)**	LME
Total Protein	Transplant * Origin + BV/ LSA + BW	Transplant * Origin + LSA **(+)** + BW	LME
Total Lipids	Transplant * Origin + BV/LSA + BW	Transplant * Origin + LSA **(+)**	LME
Mean PAR	Date * Location	Date * Location	LM
IQR PAR	Date * Location	Date * Location	LM
Mean Temperature	Date * Location	Date **(+)** + Location	LM
IQR Temperature	Date * Location	Date **(+)** * Location **(F>Sl)**	LM

Results

Initial measurements, environmental parameters, and mortality potential

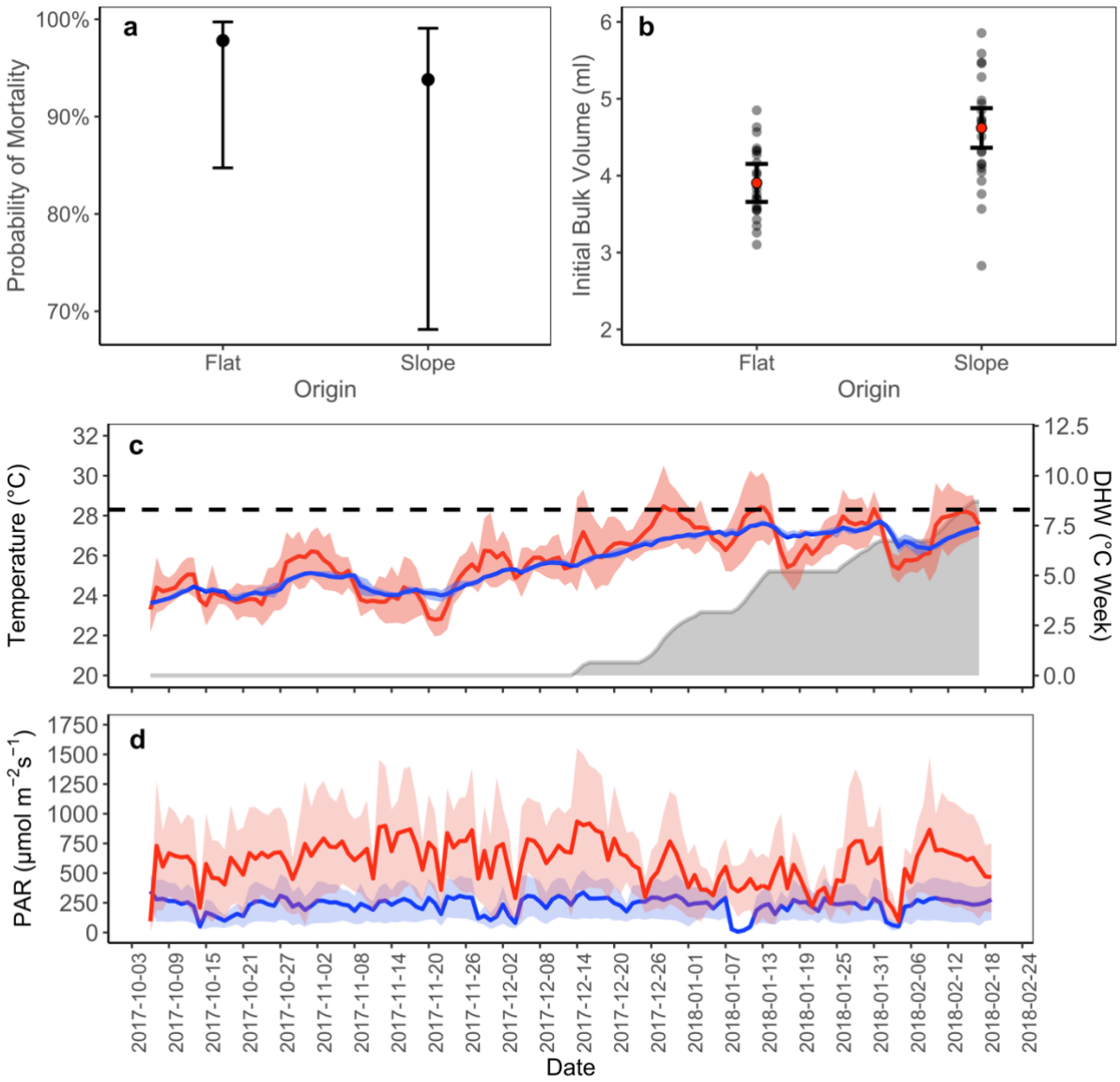

Fig 2 (a) Probability of fragment mortality by location of origin. (b) Initial differences in bulk volume (ml) between *A. formosa* fragments from each origin location ($p<0.05$), error bars represent a 95% confidence interval, grey dots show data points, and red dots indicate mean value in data set. In situ (c) 24hr mean temperature (°C) and (d) daytime mean PAR (µmol m^{-2} s^{-1}) between 6am and 6pm. For the reef slope (depth = 7-8m, blue line), and the reef flat (depth = 1-3m, red line) between the 6/10/2017 and the 17/02/2018. Ribbons on both figures represent 25th percentile (Q1) on the bottom, and 75th percentile (Q3) on the top, of daily data recorded at each location. The dashed line in figure (c) represents the local MMM + 1 (28.3°C) which is associated with bleaching threshold.

Grey area under curve indicates Q3 degree heating week (DHW) accumulation on the reef flat.

Over the length of the experimental period, corals that originated from the reef slope were 20% less likely to survive than reef flat origin corals (Anova, $\chi^2 = 4.604$, d.f. = 1, P = 0.0319, Fig 2a). This occurred over and above the random effect of live rock on mortality (fixed/random effects = 0.04/0.59). *Acropora formosa* fragments from the reef slope had significantly greater initial bulk volume than reef flat origin fragments (Anova, $F_{(1,46)}$=15.42, P=<0.001, Fig 2b).

A significant interactive effect was observed between date and location for mean PAR (Anova, $F_{(3,270)}$= 20.867, P= <0.001, Fig 2d). Mean PAR over the experimental period was always higher on the reef flat than the reef slope. An increase over the experimental period was observed at both locations but was dramatically steeper on the reef flat. Variability in PAR, measured as the interquartile range, at both locations also differed as an interactive effect of date and location (Anova, $F_{(3,270)}$= 8.852, P= 0.003, Fig 2d). As with mean PAR an increase over the experimental period was observed at both locations but was much greater on the reef flat throughout the experimental period.

Mean temperature increased over time at both sites (Anova, $F_{(3,290)}$= 830.855, P=<0.001, Fig 2d) although mean temperature did not differ between reef flat and reef slope locations. Variability, however, was significantly higher on the reef flat than on the reef slope (Anova, $F_{(3,290)}$= 125.179, P=<0.001, Fig 2d). Temperature variability significantly increased at both locations over the experimental period (Anova, $F_{(3,290)}$=9.205 , P=0.003, Fig 2c). The Q3, and mean to a lesser degree, periodically breached the MMM+1 (28.3°C) threshold established for the greater region, on the reef flat but not on the reef slope. Q3 of the reef flat breached these thresholds for periods that were sustained for less than 2 weeks 4 times over the end of the experimental period and did lead to heat accumulation as degree heating weeks (Fig 2c).

Traits associated with growth

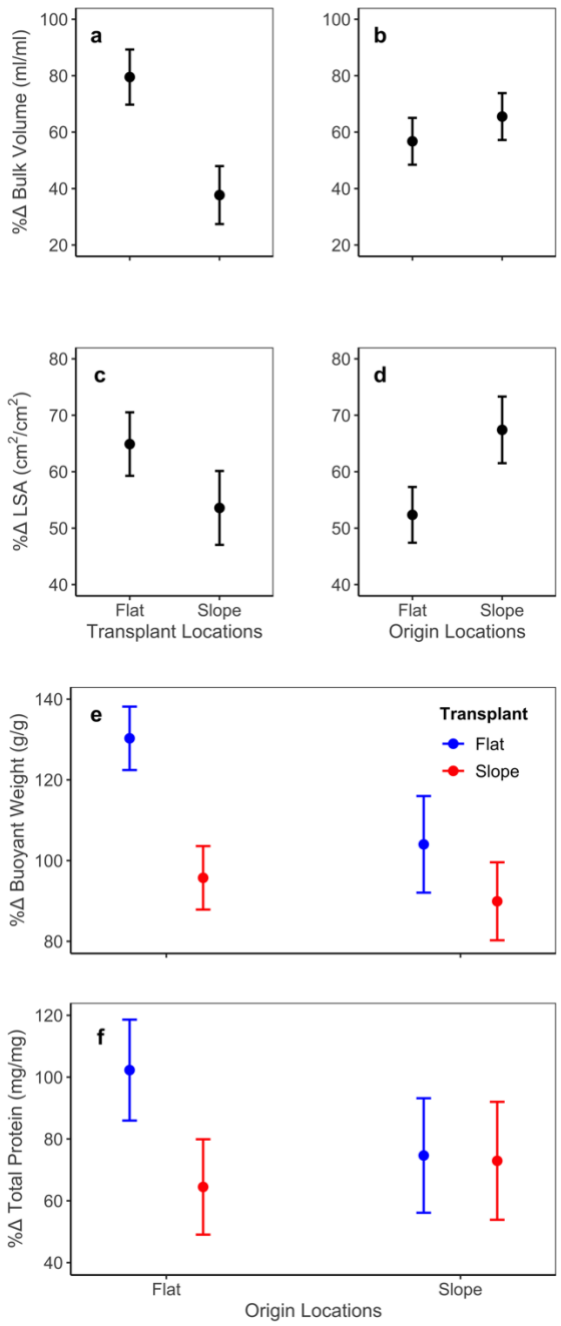

Fig 3 Change in bulk volume (ml/ml) of *A. formosa* fragments by (a) transplantation location (P<0.05), and (b) origin location (P<0.05). Change in living surface area (LSA, cm^2/cm^2) of *A. formosa* fragments by (c) transplantation location (P<0.05), and (d) origin location (P<0.05) for fixed rate of change in volume. (e) Change in buoyant weight (g/g) for fixed changes in living surface area between transplant location (flat and slope), and origin location (flat and slope). (f) Change in total proteins (mg/mg) for fixed changes in living surface area and buoyant weight between transplant location (flat and slope), and origin

location (flat and slope). Error bars in all graphs represent a 95% confidence interval. All variables are reported as percentage relative change from initial over the experimental period, as indicated by "% Δ" in all axis titles.

Acropora formosa fragments that were transplanted to the reef flat had a greater percentage change in relative bulk volume than those transplanted to the reef slope (Anova, $\chi^2 = 33.913$, d.f. = 1, $P = <0.001$, Fig 3a), irrespective of their location of origin. Location of origin had a separate significant effect on percentage change in relative bulk volume of fragments, those originating from the reef slope increased their bulk volume significantly more than those from the reef flat (Anova, $\chi^2 = 4.026$, d.f. =1, $P = 0.045$, Fig 3b).

Analysis of relative rates of change in living surface area (LSA) found that when other parameters were held constant at mean value: (i) rates of change in LSA correlated positively with rates of change in coral volume (Anova, $\chi^2 = 171.814$, d.f. = 1, $P = <0.001$); (ii) rates of change in LSA were significantly greater in corals transplanted to reef flat compared to those transplanted to reef slope (Anova, $\chi^2 = 5.601$, d.f. = 1, $P = 0.018$, Fig 3c); (iii) rates of change in LSA were significantly greater in corals of reef-slope origin than in corals of reef-flat origin (Anova, $\chi^2 = 14.708$, d.f. =1, $P = <0.001$, Fig 3d). For the same rate of change in volume, changes in coral LSA were greater in reef slope origin corals and tended to indicate increased surface rugosity as opposed to reduced partial tissue mortality.

Relative rates of change in buoyant weight (BW) between *Acropora formosa* fragments analysed when other parameters were held constant at mean value found that: (i) rates of change in BW correlated positively with rates of change in fragment LSA (Anova, $\chi^2 = 24.383$, d.f.= 1, $P = <0.001$); (ii) corals that originated from the reef flat and were transplanted to the reef flat ("Flat/Flat") had significantly higher rates of change than any other group (Anova, $\chi^2 = 4.980$, d.f.= 1, $P = 0.026$, Fig 3e), which were not significantly different from each other.

Analysis of relative rates of change in total proteins found that when other parameters were held constant at mean value: (i) rates of change in total proteins correlated positively with rates of change in LSA (Anova, $\chi^2 = 6.342$, d.f.= 1, $P = 0.012$); (ii) rates of change in total proteins were significantly greater in fragments originating from the reef flat transplanted to the reef flat, than transplanted to the reef slope (Anova, $\chi^2 = 5.046$, d.f.= 1, P

= 0.025, Fig 3f), but not different between reef slope origin corals transplanted to the reef flat or slope.

Relative rates of change in total lipids of *A. formosa* fragments when analysed with other parameters held constant at mean value were significantly correlated with LSA (Anova χ^2 = 11.948, d.f. = 1, P = <0.001). But, showed no significant effect of fragment origin or transplant location.

Discussion

Understanding the responses of coral reefs to climate change is an imperative if we are to devise effective management and policy responses to climate change. In this regard, the genetic adaptation of corals to rapidly conditions have generally been considered to be too slow to keep up with climate change (Hoegh-Guldberg 2012). Recent literature has focused on potential solutions that prevent bleaching responses of corals, through epigenetics or genetic manipulation (Oliver and Palumbi 2011; van Oppen et al. 2011) or by reducing light selectively over periods of thermal stress (Jones et al. 2016). However, reduced bleaching sensitivity may not reduce rates of coral mortality during a thermal event (Hughes et al. 2018a); and, the potential survival of these corals may not be sufficient to maintain the ecological function of coral reefs if net positive carbonate balances are not also upheld (Andersson and Gledhill 2013; Perry et al. 2013). In the present study, we set out to test an alternative hypothesis that corals survive thermal stress because they conserve energy through reducing branch extension rates that enable them to invest their energy into other processes such as into tissue production and maintenance. Investment in protein as opposed to skeletal growth leads to increased energy reserve capacities (Rodrigues and Grottoli 2007), repair and maintenance capacities and potentially even the coral's heterotrophic capacity, which at minimum requires the production of digestive enzymes to breakdown particulates for uptake over the gastrodermis.

We hypothesized that long-term exposure to the highly variable reef-flat environment would both increase survival potential and engender a conservative growth response, where greater biomass is accumulated at the cost of conserving primary calcification rates. A conservative response that would be maintained upon transplantation to the new reef slope environment. The results of our study supported our hypotheses, and thereby, suggest that epigenetic memory implanted by exposure to long-term prior stress is

unlikely to be a panacea that will save carbonate coral reefs in the short-term. It is highly likely that coral survival increased because primary calcification is to some extent relinquished. In the present study, coral properties were maintained over 4 months. Other studies, however have demonstrated that epigenetic memories can remain in some organisms for generations (Klosin et al. 2017). This conservative response, consequently, while potentially increasing coral survival, has the potential to reduce carbonate coral reef resilience, the ability of carbonate reefs to bounce back from damage incurred from any disturbance events that engenders a loss of 3D framework or carbonate from the reef ecosystem (Connell 1997). The resilience of shallow tropical reefs may slide towards that of deep-cold water reefs that are able to establish as carbonate reefs, over tens of thousands of years, only because disturbance events are rare (presently, mostly man-made and occur in the form of drag-nets), and reef erosion rates scale with reef calcification rates (Kleypas et al. 1999b; Freiwald 2002; Bongaerts et al. 2010).

The environmental contrast between the reef slope and reef flat is exhibited by the difference between the mean and variability of the recorded PAR and temperature. The high variability in temperature on the reef flat observed in this study is comparable to temperature fluctuations observed in studies identifying specific coral populations with superior thermal tolerance (Oliver and Palumbi 2011; Howells et al. 2012). Degree heating weeks (DHW) products tend to use the hottest pixels to determine regional SSTs and MMMs that are based on these SSTs (Liu et al. 2014), and we mirrored this by using the third quartile (Q3) daily temperatures which gave rise to DHWs that accumulated to 8ºC weeks over the height of summer, but only on the reef flat, not on the reef slope. Despite this apparent difference in heat stress, there was no apparent (visible) bleaching irrespective of coral origins (Fig 1), only significant mortality differences by coral origin, but not experimental location.

Whilst mean temperature between the reef flat and reef slope did not differ significantly, mean PAR did. Based on this data, we conclude that the primary difference between the deeper slope and shallower flat zones is light. However, there could be additional confounding factors such as differences in the concentration of available dissolved or particulate organic matter that were not measured, but have been described in other studies (Done 1983; Wild et al. 2004; De Goeij et al. 2013). The higher light environment of the reef flat appeared to promote primary calcification, whilst experimental

positioning on the deeper slope reduced all aspects of coral growth from primary and secondary calcification to protein accumulation. Nonetheless, reef slope origin corals experienced significantly greater primary calcification than reef flat origin corals at both experimental locations. Greater light and/or greater availability of organic nutriment may increase the energy available for growth processes to reef flat located corals relative to reef slope located corals over the long-term.

Over the experimental period of 4 months, reef flat origin corals showed a reduced ability relative to corals originating from the reef slope to acclimate to their new environment. Reef flat origin corals were unable to increase their energy acquisition to maintain the additional energy required to increase skeletal and protein densities on the slope, despite their general tendency to exhibit slow volume and tissue expansion rates. This could be, either a result of symbionts that do not acclimate to the new light environment, and/or because organic nutrients are less available at the interface between the ocean and the reef, than within a ponding reef-flat where excreted dissolved organic carbon can be enriched by microbial activity (De Goeij et al. 2013; Rix et al. 2017). By contrast, reef slope origin corals that expand relatively rapidly irrespective of location, were not apparently photo-inhibited or photo-oxidised (Richier et al. 2008) by the move to the higher light regime, but actually benefited from an apparent increase in available energy observed as a slight increase in rates of secondary calcification. This is contrary to expectations. The literature tends to argue that zooxanthellate corals can be photo-inhibited, potentially resultant from photooxidation, by increases in light, especially if light increases come in combination with increases in thermal stress (Richier et al. 2008; Skirving et al. 2018). But, many corals can acclimate over days to weeks to reduction in light (Anthony and Hoegh-Guldberg 2003; Cohen and Dubinsky 2015).

A potential reason the corals benefitted from the higher light environment in our study is that the high light habitat considered is potentially relatively richer in dissolved and particulate organic food (Wild et al, 2004, Goeij et al. 2013). Corals with thicker tissues and reduced rugosities, have been linked to a reduced ability of dinoflagellate endosymbionts to respond to external light fluxes due to the probability that the skeleton plays a lesser role in increasing the path-length of these photons (Enríquez et al. 2005). Here, host pigment and other tissue structures compete with symbionts to absorb photons (Fisher et al. 2012; Pontasch et al. 2017). This could be the optimal response of a coral subjected to highly

variable light dosing through time, that otherwise may consume significant energy as they rebuild light harvesting structures and repair D1-protein when light fluxes exceed the capacity of short-term responses such as xanthophyll cycling (Hill et al. 2011; Jeans et al. 2013). Such hosts may depend more on heterotrophy. The data from our study does not suggest that primary calcification on the reef flat is limited by the available 'head space' of water above colonies (Pandolfi et al. 2011). This experiment was performed on small fragments that were not limited by water head space at either location. Increasing water depth, is likely to reduce light levels unless corals have the capacity to keep up, and/or acclimate their energy acquisition in response to the reduction in light (Perry et al. 2018). Reef-flat origin corals in this study did not demonstrate this potential.

We have demonstrated here that conspecific of *A. formosa* that showed greater potential to survive a diversity of environments appear to exhibit a reduced ability to acclimate to changes in light availability. Attempting to further protect such corals from bleaching by periodically reducing light fields, by cloud seeding (Jones et al. 2016), would therefore impart further restrictions on energy acquisition and calcification. By contrast, the translocation of reef slope communities to the reef flat, did not generate any evidence of bleaching, despite the significant increase in the light field and regular incursions into stressful temperatures. Given that the mortality rate of these corals did not vary by location, the evidence suggests that Acroporids originating from the reef slope acclimate to the changing light regime relatively quickly (21 days; Anthony and Hoegh-Guldberg 2003; Jeans et al. 2013). Rapid photo-acclimation however has significant ramifications on the efficacy and practicality of applying shade to protect such corals should they be exposed to greater heat stress. Shade is intended to reduce excitation pressure at PSII and prevent the photo-oxidation to the Symbiodiniaceae photosystems, but if these photosystems rapidly increase the efficiency of photon capture in response to reductions in the light field, then shade will not serve to reduce excitation pressure. Shading will however consume additional energy as symbionts would need to invest in rebuilding their light harvesting antennae (Stambler and Dubinsky; Titlyanov et al. 2001), potentially reducing quanta of energy translocation to host.

On a more positive note, reef flat coral transferred back to the reef flat had higher skeletal density relative to other treatments, whilst also maximising protein density. Consequentially, primary calcification was reduced. Increases in skeletal density can reduce

fragmentation and over the long-term (Lirman 2000; Okubo et al. 2007), even colonies with limited primary calcification can accumulate to cover a large area in space as long as physical forces do not exceed the strength of the produced skeleton (Scoffin et al. 1992). Notably lower expansion rates would be beneficial to the maintenance of symbiont densities, as the need for production of new symbionts to occupy the new material would be reduced. Rapid outward expansion is reportedly associated with “bleached” coral tissue (Oliver 1984). Clearly, some of these hypotheses regarding the explanation of the observed responses require testing. If epigenetic memory is responsible for increasing the survival of reef flat corals exposed to highly variable environments, then environments that tandem variability in light and temperature, in addition to many other abiotic variables, result in corals that sacrificed calcification (Denis et al. 2011, 2013). Survival appears not to be based on the reduced ability to bleach, but rather correlates with reductions in volume and tissue expansion in the Acroporid coral tested. Other corals (Gold and Palumbi 2018), may maintain rates of linear extension, but it is questionable whether other aspects of calcification are not compromised. For example, reef flat and reef slope conspecifics of *A. formosa* from this study, clipped to the same length, have different volumes and skeletal densities that forced the use of relative changes to preserve the statistical assumption that covariates are independent of treatment effect.

Presently, we assume that the differences observed between these relatively proximal *A. formosa* populations are driven by epigenetic consequences associated with prior long-term exposure to different abiotic environments within the reef-scape. There is, however, the potential that the relative inflexibility of the two coral populations to alter properties when exposed to new environments has a genetic cause. The two populations may hide cryptic speciation, a phenomenon that is increasingly observed amongst coral taxa (Rosser 2016; Gold and Palumbi 2018; van Oppen et al. 2018). For cryptic speciation to occur amongst spawning populations that are relatively proximal in space, gene flow may be limited (Nosil and Crespi 2004). In this regard, temperature can change the timing of spawning (Keith et al. 2016), and asynchronous spawning can inhibit gene flow (Rosser 2016). Alternatively, cryptic species could exhibit different larval and settlement properties that reinforce differential recruitment in these zones (Combosch and Vollmer 2011). In a brooding species, *Seriatopora hystrix* genetic isolation has been observed to result from differences in reproductive timing between populations in deep and shallow habitats (Bongaerts et al. 2011, 2020). More recently the same has been determined for *Pocillopora*

damicornis, (van Oppen et al. 2018). Interestingly, this genetic differentiation in *P. damicornis* was observed on Heron Island over similar geographic distances as in the current study. However, *P. damicornis* is a brooding species while the target species in the current study, *A. formosa*, is a broadcasting species (ref).

Corals that have a prior life history of chronic exposure to highly variable environments tend to be less susceptible to mortality. In this study, we observed that corals raised to adult colonies on the reef flat have a greater survival potential in any environment than conspecifics raised on the reef slope. Daily third quartile temperature accumulated to 8°Cweek over the summer on the reef flat. In combination with an increased irradiance for reef slope origin corals moved to the reef flat, the new environment however did not increase bleaching susceptibility of these reef slope origin corals. Rather, they demonstrated that coral growth in these slope origin corals was suppressed by the lower light conditions under which they appear to nonetheless flourish on the reef slope. The greater survival potential of reef flat origin corals was correlated to their having greater tissue thickness likely facilitated by reduced rates of primary and secondary calcification. Furthermore, these reef flat origin corals failed to acclimate to the lower light levels offered on the reef slope as suggested by a lack of energy to maintain high tissue protein densities despite reduced branch expansion. The fact that reef flat origin corals to not physiologically morph into reef slope origin corals upon relocation to the reef slope and vice-versa suggests that these corals have become epigenetic or genetically distinct populations. The study supports the hypothesis that exposure to a highly variable environment results in “tough” corals, but it identifies that one of the costs of increased survival potential is reduced calcification. These “super corals” therefore lack the properties that are required to save carbonate reefs exposed to increases in the intensity and frequency of disturbance events as a result of climate change. Further, they lack the ability to respond positively to the reductions in light field likely associated with future sea-level rise. Branching Acroporids are important to the 3-dimensional structure and many services provided by carbonate reefs. The present study suggests that the characteristic that allow corals to survive and prosper in highly variable reef environments, do not align with those that are required to maintain carbonate coral reefs exposed to the many consequences of climate change.

Acknowledgements

We thank the members of the CRE laboratory at UQ, especially Aaron Chai, for assistance with coral collection and preparation. Draft reviews by Ove Hoegh-Guldberg and Catherine Kim improved the manuscript. The experiment was funded by the Australian Research Council (ARC) and by the National Oceanic and Atmospheric Administration (NOAA) via ARC Centre of Excellence for Coral Reef Studies CE140100020 (S.D and O.H-G) and ARC Linkage LP110200874 (O.H-G and S.D.).

References

Albright R, Anthony KRN, Baird M, Beeden R, Byrne M, Collier C, Dove S, Fabricius K, Hoegh-Guldberg O, Kelly RP, Lough J, Mongin M, Munday PL, Pears RJ, Russell BD, Tilbrook B, Abal E (2016) Ocean acidification: Linking science to management solutions using the Great Barrier Reef as a case study. J Environ Manage 182:641–650

Albright R, Benthuysen J, Cantin N, Caldeira K, Anthony K (2015) Coral reef metabolism and carbon chemistry dynamics of a coral reef flat. Geophys Res Lett 42:3980–3988

Allemand D, Tambutté É, Zoccola D, Tambutté S (2011) Coral calcification, cells to reefs. In: Dubinsky Z., Stambler N. (eds) Coral Reefs: An Ecosystem in Transition. Springer, New York, pp 119–150

Andersson AJ, Gledhill D (2013) Ocean acidification and coral reefs: Effects on breakdown, dissolution, and net ecosystem calcification. Ann Rev Mar Sci 5:321–348

Anthony KRN, Connolly SR, Willis BL (2002) Comparative analysis of energy allocation to tissue and skeletal growth in corals. Limnol Oceanogr 47:1417–1429

Anthony KRN, Hoegh-Guldberg O (2003) Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: An analogue to plants in forest gaps and understoreys? Funct Ecol 17:246–259

Anthony KRN, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R (2009) Energetics approach to predicting mortality risk from environmental stress: A case study of coral bleaching. Funct Ecol 23:539–550

Berkelmans R, Van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: A “nugget of hope” for coral reefs in an era of climate change. Proc R Soc B Biol Sci 273:2305–2312

Bongaerts P, Ir C, Ying H, Wels D, S H Den (2020) Cryptic diversity masks ecologically distinct coral species on tropical reefs. 1–24

Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the “deep reef refugia” hypothesis: Focus on Caribbean reefs. Coral Reefs 29:1–19

Bongaerts P, Riginos C, Hay KB, Van Oppen MJ, Hoegh-Guldberg O, Dove S (2011) Adaptive divergence in a scleractinian coral: Physiological adaptation of Seriatopora hystrix to shallow and deep reef habitats. BMC Evol Biol 11:303

Bradbury RH (1981) Energy , on a Coral Reef Ecosystem. Mar Ecol 5:229–241

Brown KT, Bender-Champ D, Kubicek A, van der Zande R, Achlatis M, Hoegh-Guldberg O, Dove SG (2018) The dynamics of coral-algal interactions in space and time on the southern Great Barrier Reef. Front Mar Sci 5:1–13

Bucher DJ, Harriott VJ, Roberts LG (1998) Skeletal micro-density, porosity and bulk density of acroporid corals. J Exp Mar Bio Ecol 228:117–136

Cleves PA, Strader ME, Bay LK, Pringle JR, Matz M V. (2018) CRISPR/Cas9-mediated genome editing in a reef-building coral. Proc Natl Acad Sci U S A 115:5235–5240

Cohen AL, Holcomb M (2009) Why corals care about ocean acidification uncovering the mechanism. Oceanography 22:118–127

Cohen I, Dubinsky Z (2015) Long term photoacclimation responses of the coral Stylophora pistillata to reciprocal deep to shallow transplantation: Photosynthesis and calcification. Front Mar Sci 2:1–13

Coles SL, Jokiel PL (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. Mar Biol 43:209–216

Combosch DJ, Vollmer S V. (2011) Population genetics of an ecosystem-defining reef coral Pocillopora damicornis in the Tropical Eastern Pacific. PLoS One 6:

Connell JH (1997) Disturbance and recovery of coral assemblages. Coral Reefs 16:101–113

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461–488

Darling ES, Côté IM (2018) Seeking resilience in marine ecosystems. Science (80-) 359:986–987

Denis V, Debreuil J, De Palmas S, Richard J, Guillaume MMM, Bruggemann JH (2011) Lesion regeneration capacities in populations of the massive coral porites lutea at réunion island: Environmental correlates. Mar Ecol Prog Ser 428:105–117

Denis V, Guillaume MMM, Goutx M, de Palmas S, Debreuil J, Baker AC, Boonstra RK, Bruggemann JH (2013) Fast Growth May Impair Regeneration Capacity in the Branching Coral Acropora muricata. PLoS One 8:4–10

Done TJ (1983) Coral zonation: its nature and significance. In: Barnes D.J., Clouston B. (eds) Perspectives on coral reefs. Australian Institue of Marin Science, pp 107–147

Dove S, Ortiz JC, Enríquez S, Fine M, Fisher P, Iglesias-Prieto R, Thornhill D, Hoegh-Guldberg O (2006) Response of holosymbiont pigments from the scleractinian coral Montipora monasteriata to short-term heat stress. Limnol Oceanogr 51:1149–1158

Dunn SR, Thomas MC, Nette GW, Dove SG (2012) A Lipidomic Approach to Understanding Free Fatty Acid Lipogenesis Derived from Dissolved Inorganic Carbon within Cnidarian-Dinoflagellate Symbiosis. PLoS One 7:e46801

Enríquez S, Méndez ER, Iglesias-Prieto R (2005) Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnol Oceanogr 50:1025–1032

Fisher PL, Malme MK, Dove S (2012) The effect of temperature stress on coral-Symbiodinium associations containing distinct symbiont types. Coral Reefs 31:473–485

Fisher R, Bessell-Browne P, Jones R (2019) Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. Nat Commun 10:

Flynn KJ, Stoecker DK, Mitra A, Raven JA, Glibert PM, Hansen PJ, Granéli E, Burkholder JM (2013) Misuse of the phytoplankton-zooplankton dichotomy: The need to assign organisms as mixotrophs within plankton functional types. J Plankton Res 35:3–11

Freiwald A (2002) Reef-Forming Cold-Water Corals. Ocean Margin Systems. Springer Berlin Heidelberg, pp 365–385

Georgiou L, Falter J, Trotter J, Kline DI, Holcomb M, Dove SG, Hoegh-Guldberg O, McCulloch M (2015) PH homeostasis during coral calcification in a free ocean CO2 enrichment (FOCE) experiment, Heron Island reef flat, Great Barrier Reef. Proc Natl Acad Sci U S A 112:13219–13224

De Goeij JM, Van Oevelen D, Vermeij MJA, Osinga R, Middelburg JJ, De Goeij AFPM, Admiraal W (2013) Surviving in a marine desert: The sponge loop retains resources within coral reefs. Science (80-) 342:108–110

Gold Z, Palumbi SR (2018) Long-term growth rates and effects of bleaching in Acropora hyacinthus. Coral Reefs 37:267–277

Gourlay MR (Michael R, Jell JS (1992) Heron Island spoil dump : report on short term monitoring and environmental effects. Dept. of Civil Engineering, St. Lucia, Qld.

Grottoli AG, Rodrigues LJ (2011) Bleached Porites compressa and Montipora capitata corals catabolize δ13C-enriched lipids. Coral Reefs 30:687–692

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189

Grottoli AG, Tchernov D, Winters G (2017) Physiological and biogeochemical responses of super-corals to thermal stress from the northern gulf of Aqaba, Red Sea. Front Mar Sci 4:

Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, Mcginley M, Baumann J, Matsui Y (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. Glob Chang Biol 20:3823–3833

Highsmith R (1982) Reproduction by Fragmentation in Corals. Mar Ecol Prog Ser 7:207–226

Hill R, Brown CM, DeZeeuw K, Campbell DA, Ralph PJ (2011) Increased rate of D1 repair in coral symbionts during bleaching is insufficient to counter accelerated photo-inactivation. Limnol Oceanogr 56:139–146

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839–866

Hoegh-Guldberg O (2012) The adaptation of coral reefs to climate change: Is the Red Queen being outpaced? Sci Mar 76:403–408

Hoegh-Guldberg O, Jacob D, Taylor M, Guillén Bolaños T, Bindi M, Brown S, Camilloni IA, Diedhiou A, Djalante R, Ebi K, Engelbrecht F, Guiot J, Hijioka Y, Mehrotra S, Hope CW, Payne AJ, Pörtner HO, Seneviratne SI, Thomas A, Warren R, Zhou G (2019) The human imperative of stabilizing global climate change at 1.5°C. Science (80-) 365:

Hoegh-Guldberg O, Jones RJ, Ward S, Loh WK, Baker AC (2002) Communicating arising ecology: Is coral bleaching really adaptive? Nature 415:601–602

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Hoegh-Guldberg O, Ortiz JC, Dove S (2011) The future of coral reefs. Science (80-) 334:1494–1495

Hoegh Guldberg O, Salvat B (1995) Periodic mass-bleaching and elevated sea temperatures: Bleaching of outer reef slope communities in Moorea, French Polynesia. Mar Ecol Prog Ser 121:181–190

Holmes G (2008) Estimating three-dimensional surface areas on coral reefs. J Exp Mar Bio Ecol 365:67–73

Hoogenboom MO, Connolly SR, Anthony KRN (2008) Interactions between morphological and physiological plasticity optimize energy acquisition in corals. Ecology 89:1144–1154

Howells EJ, Beltran VH, Larsen NW, Bay LK, Willis BL, Van Oppen MJH (2012) Coral thermal tolerance shaped by local adaptation of photosymbionts. Nat Clim Chang 2:116–120

Howells EJ, Berkelmans R, Van Oppen MJH, Willis BL, Bay LK (2013) Historical thermal regimes define limits to coral acclimatization. Ecology 94:1078–1088

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science (80-) 359:80–83

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS, Torda G (2018b) Global warming transforms coral reef

assemblages. Nature 556:492–496
Iglesias-Prieto R, Trench RK (1997) Acclimation and adaptation to irradiance in symbiotic dinoflagellates. II. Response of chlorophyll-protein complexes to different photon-flux densities. Mar Biol 130:23–33
IPCC (2014) Climate Change 2014: Mitigation of Climate Change. Summary for Policymakers and Technical Summary. Clim Chang 2014 Mitig Clim Chang Part Work Gr III Contrib to Fifth Assess Rep Intergov Panel Clim Chang 1–161
Jeans J, Campbell DA, Hoogenboom MO (2013) Increased reliance upon photosystem II repair following acclimation to high-light by coral-dinoflagellate symbioses. Photosynth Res 118:219–229
Jell JS, Flood PG (1978) Guide to the geology of reefs of the Capricorn and Bunker groups, Great Barrier Reef province with special reference to the Heron Reef. Pap Dep Geol Univ Queensl 8:85
Jell JS, Webb GE (2012) Geology of Heron Island and adjacent reefs, great barrier reef, Australia. Episodes 35:110–119
Jeong HJ, Yoo Y Du, Kang NS, Lim AS, Seong KA, Lee SY, Lee MJ, Lee KH, Kim HS, Shin W, Nam SW, Yih W, Lee K (2012) Heterotrophic feeding as a newly identified survival strategy of the dinoflagellate Symbiodinium. Proc Natl Acad Sci U S A 109:12604–12609
John A, Weisberg S, Price B, Adler D, Bates D, Baud-bovy G, Bolker B, Ellison S, Firth D, Friendly M, Gorjanc G, Graves S, Heiberger R, Krivitsky P, Laboissiere R, Maechler M, Monette G, Murdoch D, Nilsson H, Ogle D, Ripley B, Venables W, Walker S, Winsemius D, Zeileis A, R-Core (2020) Companion to Applied Regression Depends. R Packag Version 20-21 1–149
Jokiel PL, Rodgers KS, Kuffner IB, Andersson AJ, Cox EF, Mackenzie FT (2008) Ocean acidification and calcifying reef organisms: A mesocosm investigation. Coral Reefs 27:473–483
Jones A, Berkelmans R (2010) Potential costs of acclimatization to a warmer climate: Growth of a reef coral with heat tolerant vs. sensitive symbiont types. PLoS One 5:
Jones AM, Berkelmans R (2011) Tradeoffs to Thermal Acclimation: Energetics and Reproduction of a Reef Coral with Heat Tolerant Symbiodinium Type-D . J Mar Biol 2011:1–12
Jones ISF, Wheen RJ, Ridley JD, Harrison DP, Lawrence MW (2016) A method for saving coral reefs from bleaching by cloud intensification.
Keith SA, Maynard JA, Edwards AJ, Guest JR, Bauman AG, van Hooidonk R, Heron SF, Berumen ML, Bouwmeester J, Piromvaragorn S, Rahbek C, Baird AH (2016) Coral mass spawning predicted by rapid seasonal rise in ocean temperature. Proc R Soc B Biol Sci 283:lt;xocs:firstpage xmlns:xocs=""/>
Kinsey E (1967) July 25, 19661. 23–34
Kleypas JA, Buddemeier RW, Archer D, Gattuso J, Langdon C, Opdyke BN, Kleypas JA, Buddemeier RW, Archer D, Gattuso J, Langdon C, Opdyke BN (1999a) Geochemical Consequences of Increased Atmospheric Carbon Dioxide on Coral Reefs Published by : American Association for the Advancement of Science Stable URL : http://www.jstor.org/stable/2899149 Linked references are available on JSTOR for this article : 284:118–120
Kleypas JA, McManu JW, Mene LAB (1999b) Environmental limits to coral reef development: Where do we draw the line? Am Zool 39:146–159
Kline DI, Teneva L, Schneider K, Miard T, Chai A, Marker M, Headley K, Opdyke B, Nash M, Valetich M, Caves JK, Russell BD, Connell SD, Kirkwood BJ, Brewer P, Peltzer E, Silverman J, Caldeira K, Dunbar RB, Koseff JR, Monismith SG,

Mitchell BG, Dove S, Hoegh-Guldberg O (2012) A short-term in situ CO 2 enrichment experiment on Heron Island (GBR). Sci Rep 2:1–9

Klosin A, Casas E, Hidalgo-Carcedo C, Vavouri T, Lehner B (2017) Transgenerational transmission of environmental information in C. elegans. Science (80-) 356:320–323

Leuzinger S, Willis BL, Anthony KRN (2012) Energy allocation in a reef coral under varying resource availability. Mar Biol 159:177–186

Levin RA, Voolstra CR, Agrawal S, Steinberg PD, Suggett DJ, van Oppen MJH (2017) Engineering strategies to decode and enhance the genomes of coral symbionts. Front Microbiol 8:1–11

Lirman D (2000) Fragmentation in the branching coral Acropora palmata (Lamarck): Growth, survivorship, and reproduction of colonies and fragments. J Exp Mar Bio Ecol 251:41–57

Lirman D, Schopmeyer S, Galvan V, Drury C, Baker AC, Baums IB (2014) Growth dynamics of the threatened caribbean staghorn coral acropora cervicornis: Influence of host genotype, symbiont identity, colony size, and environmental setting. PLoS One 9:e107253

Liu G, Heron SF, Mark Eakin C, Muller-Karger FE, Vega-Rodriguez M, Guild LS, de la Cour JL, Geiger EF, Skirving WJ, Burgess TFR, Strong AE, Harris A, Maturi E, Ignatov A, Sapper J, Li J, Lynds S (2014) Reef-scale thermal stress monitoring of coral ecosystems: New 5-km global products from NOAA coral reef watch. Remote Sens 6:11579–11606

Lüdecke D (2014) sjPlot: sjPlot - data visualization for statistics in social science. R Packag version 240 2016

Magnan AK, Colombier M, Billé R, Joos F, Hoegh-Guldberg O, Pörtner HO, Waisman H, Spencer T, Gattuso JP (2016) Implications of the Paris agreement for the ocean. Nat Clim Chang 6:732–735

Mieog JC, Olsen JL, Berkelmans R, Bleuler-Martinez SA, Willis BL, van Oppen MJH (2009) The roles and interactions of symbiont, host and environment in defining coral fitness. PLoS One 4:e6364

Mulholland MR, Morse R, Egerton T, Bernhardt PW, Filippino KC (2018) Blooms of Dinoflagellate Mixotrophs in a Lower Chesapeake Bay Tributary: Carbon and Nitrogen Uptake over Diurnal, Seasonal, and Interannual Timescales. Estuaries and Coasts 41:1744–1765

Naumann MS, Niggl W, Laforsch C, Glaser C, Wild C (2009) Coral surface area quantification-evaluation of established techniques by comparison with computer tomography. Coral Reefs 28:109–117

Nosil P, Crespi BJ (2004) Does gene flow constrain adaptive divergence or vice versa? A test using ecomorphology and sexual isolation in Timema cristinae walking-sticks. Evolution (N Y) 58:102–112

Okubo N, Motokawa T, Omori M (2007) When fragmented coral spawn? Effect of size and timing on survivorship and fecundity of fragmentation in Acropora formosa. Mar Biol 151:353–363

Oliver JK (1984) Intra-colony variation in the growth of Acropora formosa: extension rates and skeletal structure of white (zooxanthellae-free) and brown-tipped branches. Coral Reefs 3:139–147

Oliver TA, Palumbi SR (2011) Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs 30:429–440

van Oppen MJH, Bongaerts P, Frade P, Peplow LM, Boyd SE, Nim HT, Bay LK (2018) Adaptation to reef habitats through selection on the coral animal and its associated

microbiome. Mol Ecol 27:2956–2971
Van Oppen MJH, Oliver JK, Putnam HM, Gates RD (2015) Building coral reef resilience through assisted evolution. Proc Natl Acad Sci U S A 112:2307–2313
van Oppen MJH, Souter P, Howells EJ, Heyward A, Berkelmans R (2011) Novel genetic diversity through somatic mutations: Fuel for adaptation of reef corals? Diversity 3:405–423
Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014) Mechanisms of reef coral resistance to future climate change. Science (80-) 344:895–898
Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. Science (80-) 333:418–422
Perry CT, Alvarez-Filip L, Graham NAJ, Mumby PJ, Wilson SK, Kench PS, Manzello DP, Morgan KM, Slangen ABA, Thomson DP, Januchowski-Hartley F, Smithers SG, Steneck RS, Carlton R, Edinger EN, Enochs IC, Estrada-Saldívar N, Haywood MDE, Kolodziej G, Murphy GN, Pérez-Cervantes E, Suchley A, Valentino L, Boenish R, Wilson M, MacDonald C (2018) Loss of coral reef growth capacity to track future increases in sea level. Nature 558:396–400
Perry CT, Murphy GN, Kench PS, Smithers SG, Edinger EN, Steneck RS, Mumby PJ (2013) Caribbean-wide decline in carbonate production threatens coral reef growth. Nat Commun 4:1402
Pontasch S, Fisher PL, Krueger T, Dove S, Hoegh-Guldberg O, Leggat W, Davy SK (2017) Photoacclimatory and photoprotective responses to cold versus heat stress in high latitude reef corals. J Phycol 53:308–321
Potts DC, Swart PK (1984) Water temperature as an indicator of environmental variability on a coral reef. Limnol Oceanogr 29:504–516
Puill-Stephan E, van Oppen MJH, Pichavant-Rafini K, Willis BL (2012) High potential for formation and persistence of chimeras following aggregated larval settlement in the broadcast spawning coral, Acropora millepora. Proc R Soc B Biol Sci 279:699–708
Putnam HM, Davidson JM, Gates RD (2016) Ocean acidification influences host DNA methylation and phenotypic plasticity in environmentally susceptible corals. Evol Appl 9:1165–1178
Richier S, Cottalorda JM, Guillaume MMM, Fernandez C, Allemand D, Furla P (2008) Depth-dependant response to light of the reef building coral, Pocillopora verrucosa: Implication of oxidative stress. J Exp Mar Bio Ecol 357:48–56
Rix L, de Goeij JM, van Oevelen D, Struck U, Al-Horani FA, Wild C, Naumann MS (2017) Differential recycling of coral and algal dissolved organic matter via the sponge loop. Funct Ecol 31:778–789
Rodrigues LJ, Grottoli AG (2007) Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnol Oceanogr 52:1874–1882
Rosser NL (2016) Demographic history and asynchronous spawning shape genetic differentiation among populations of the hard coral Acropora tenuis in Western Australia. Mol Phylogenet Evol 98:89–96
Rowan B, Knowlton N (1995) Intraspecific diversity and ecological zonation in coral-algal symbiosis. Proc Natl Acad Sci U S A 92:2850–2853
Rowan R, Knowlton N, Baker A, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature 388:265–269
Santos IR, Glud RN, Maher D, Erler D, Eyre BD (2011) Diel coral reef acidification driven by porewater advection in permeable carbonate sands, Heron Island, Great Barrier Reef. Geophys Res Lett 38:
Scoffin TP, Tudhope AW, Brown BE, Chansang H, Cheeney RF (1992) Patterns and

possible environmental controls of skeletogenesis of Porites lutea, South Thailand. Coral Reefs 11:1–11

Skirving W, Enríquez S, Hedley JD, Dove S, Eakin CM, Mason RAB, Cour JLD La, Liu G, Hoegh-Guldberg O, Strong AE, Mumby PJ, Iglesias-Prieto R (2018) Remote sensing of coral bleaching using temperature and light: Progress towards an operational algorithm. Remote Sens 10:

Smale DA, Wernberg T, Oliver ECJ, Thomsen M, Harvey BP, Straub SC, Burrows MT, Alexander L V., Benthuysen JA, Donat MG, Feng M, Hobday AJ, Holbrook NJ, Perkins-Kirkpatrick SE, Scannell HA, Sen Gupta A, Payne BL, Moore PJ (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Chang 9:306–312

Smith DJ, Suggett DJ, Baker NR (2005) Is photoinhibition of zooxanthellae photosynthesis the primary cause of thermal bleaching in corals? Glob Chang Biol 11:1–11

Spencer Davies P (1989) Short-term growth measurements of corals using an accurate buoyant weighing technique. Mar Biol 101:389–395

Spurgeon JPG (1992) The Economic Valuation of Coral Reefs. Mar Pollut Bull 24:529–536

Stambler N, Dubinsky Z Corals as light collectors: an integrating sphere approach.

Stanley GD (2006) Photosymbiosis and the evolution of modern coral reefs. Science (80-) 312:857–858

Steen RG (1986) Evidence for Heterotrophy By Zooxanthellae in Symbiosis With Aiptasia Pulchella. Biol Bull 170:267–278

Steen RG (1987) Evidence for facultative heterotrophy in cultured zooxanthellae. Mar Biol 95:15–23

Szmant AM, Gassman NJ (1990) The effects of prolonged “bleaching” on the tissue biomass and reproduction of the reef coral Montastrea annularis. Coral Reefs 8:217–224

Tanaka Y, Miyajima T, Koike I, Hayashibara T, Ogawa H (2007) Imbalanced coral growth between organic tissue and carbonate skeleton caused by nutrient enrichment. Limnol Oceanogr 52:1139–1146

Thomas L, Rose NH, Bay RA, López EH, Morikawa MK, Ruiz-Jones L, Palumbi SR (2018) Mechanisms of Thermal Tolerance in Reef-Building Corals across a Fine-Grained Environmental Mosaic: Lessons from Ofu, American Samoa. Front Mar Sci 4:1–15

Titlyanov EA, Titlyanova T V., Yamazato K, Van Woesik R (2001) Photo-acclimation dynamics of the coral Stylophora pistillata to low and extremely low light. J Exp Mar Bio Ecol 263:211–225

Veal CJ, Holmes G, Nunez M, Hoegh-Guldberg O, Osborn J (2010) A comparative study of methods for surface area and three dimensional shape measurement of coral skeletons. Limnol Oceanogr Methods 8:241–253

Veron JEN (John EN (1993) Corals of Australia and the Indo-Pacific. University of Hawaii Press, Honolulu

Weeks SJ, Anthony KRN, Bakun A, Feldman GC, Hoegh-Guldberg O (2008) Improved predictions of coral bleaching using seasonal baselines and higher spatial resolution. Limnol Oceanogr 53:1369–1375

Whitaker JR, Granum PE (1980) An absolute method for protein determination based on difference in absorbance at 235 and 280 nm. Anal Biochem 109:156–159

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer International Publishing, Cham

Wild C, Huettel M, Klueter A, Kremb SG, Rasheed MYM, Jørgensen BB (2004) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. Nature 428:66–70